

Variation in Tree Fern Stipe Length with Canopy Height: Tracking Preferred Habitat Through Morphological Change

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ABSTRACT.—*Cyathea caracasana* is a common open-habitat tree fern in the Andes of Colombia. In full sun, stem growth rates are high (up to 2 cm/month) and individuals regularly produce spores. However, even the fastest growing ferns are overtopped by woody angiosperms after 10 to 15 years of natural forest regeneration. As individuals are overtopped, *C. caracasana* produces nearly vertical fronds with long stipes (commonly over 3 m) apparently to place the photosynthetic surface into the canopy. We compared stipe length and blade length and width among individuals growing in open sites and in the understories of two regenerating forests: one with a canopy of 20–25 m, and one with a canopy of 5–8 m. Stipes and blades were shortest in open habitat and longest in the low-canopy forest. Ferns in the high-canopy forest had intermediate measurements. Despite the change in frond length, the number of primary pinnae per-frond did not differ among the habitats sampled. This suggests that elongation cues are received late in the development of the frond. This conclusion is supported by a positive relationship between stipe length and the distance of the fern meristem below the canopy. Because both understory populations show stipe elongation relative to open-habitat ferns, the cue to elongate is likely a low red/far-red wavelength ratio of the light received by the apical meristem. Extraordinary elongation is probably made possible by extra carbon resources available to low-canopy plants, which still have leaves in full sun. This sense and response mechanism allows individual plants to produce elongated fronds as their apical meristems are overtopped. Functionally, the long-stiped plants remain in full sun even after they are overtopped, thus they “track” their preferred, open habitat.

Plant populations respond to environmental variation in several ways. When the environment fluctuates infrequently relative to the life span of individuals, adaptive segregation may produce differential response to environmental cues among separate populations. Consider variation in light environment. Sun-adapted populations of *Impatiens capensis* L. showed enhanced growth in response to changes in the ratio of red (600–700 nm) to far-red (700–850 nm) light relative to shade-adapted populations (Dudley and Schmitt, 1995). Similar sun/shade segregation in growth response to red/far-red (R/FR) has been observed in many angiosperm species in open (as compared to understory) communities (Morgan and Smith, 1979). In contrast, when the environment varies frequently relative to the life span of individuals, adaptive segregation cannot occur and individuals must rely on morphological and physiological flexibility (plasticity) (Thompson, 1991; Sultan, 1993; Ackerly and Bazzaz, 1995; Arens, 1997). In such cases, plants may change form or physiology to suit new conditions, for example switching from sun-leaf to shade-leaf anatomy (Arens, 1997). Alternatively, individuals “track” or follow their preferred habitat as it moves. Conventionally, habitat-tracking in plants has been applied to intergenerational migration (Davis et al., 1986; Webb, 1987; Davis and Sa-



FIG. 1. Location of La Reserva Natural La Planada within Colombia, South America.

binski, 1992). Within the life span of a clonal plant, differential growth allows modules to follow resources (Salzman, 1985; Slade and Hutchings, 1987). This form of habitat-tracking may also be applied to differential organ growth in non-clonal plants.

When growing in low-canopy secondary forest, some individuals of the tree fern *Cyathea caracasana* (Klotzsch) Domin produce unusually long, vertically oriented stipes that place the photosynthetic portion of the frond into the canopy, where it experiences full sun. This paper documents our observation as an example of habitat-tracking by means of changing allometric growth of individual plant organs.

STUDY SITE AND METHODS

La Reserva Natural La Planada is located between 1,850 m and 2,300 m above sea level on the Pacific slope of the Andean Cordillera in Nariño, Colombia, 1°09'37"N, 77°59'13"W (Fig. 1). La Planada receives about 4,500 mm

of rainfall annually (cumulative data from 1982 to 1997) with a “dry” season from June to August. Cloud-harvesting approximately doubles the moisture available to plants (C. Ríos, Instituto von Humboldt, Villa de Leyva, Colombia, unpublished data). Average daily temperature is 19°C, with no seasonal variation. Vegetation within the reserve is typical of Pacific slope cloud forest at this elevation, with a natural canopy approximately 25 m in height composed of relatively few tree species. The most common canopy trees include *Alchornea* (Euphorbiaceae), *Clusia* (Guttiferae), *Inga* (Fabaceae), *Miconia* (Melastomataceae), *Myrica* and *Psidium* (Myrtaceae), and *Otoba* (Myristicaceae). Eleven described tree fern species have been reported from the reserve (Arens and Sánchez Baracaldo, 1998). The majority of the reserve’s 3,200 hectares are covered with primary forest that has been little-disturbed by human activity.

Within primary forest, canopy gaps are an important part of the habitat dynamic. Primary forest turnover due to gap formation and canopy closure was estimated at 3% annually (Samper K., 1992). This suggests that at a given point in the forest, a canopy gap will open every 30 years, on average—well within the life span of most tree ferns. The reserve also contains areas of recently abandoned pasture and secondary forest, which represent less than 50 years of natural regeneration. Secondary forest was identified by relatively homogeneous size class of canopy trees; land-use records establish the time of abandonment. Regeneration of abandoned pasture is rapid, with canopies of 5 to 6 meters closing within 10 to 20 years after abandonment. Land use history information available at the reserve permits precise estimation of regeneration-time. This makes La Planada a valuable site for studies of successional dynamics in the cloud forest ecosystem.

Field work was initiated in 1992 and completed in 1994. We identified co-occurring individuals of *Cyathea caracasana* whose apical meristems experienced three distinct habitats: (1) open habitat, (2) the understory of 35-year-old secondary forest, and (3) the understory of 10-year-old secondary forest. Open habitat plants grew in recently abandoned pasture and cleared areas, commonly within 1,000 m of reserve buildings. Abandoned pastures were in the earliest stages of forest regeneration. Vegetation was characterized by grasses, herbaceous angiosperms, moss, lycophytes, ferns, and *Miconia* saplings. In open habitat, tree ferns grew in full sun. Understory individuals grew in the shade below the closed canopy of secondary forest (approximately 35 years of regeneration); this sample is referred to as “high canopy” forest in subsequent discussion. The canopy was approximately 25 m in height with no emergent trees. Canopy gaps were uncommon and none were observed greater than 2 m in diameter. The younger secondary forest represented approximately 10 years of regeneration based on land-use history records, and had a multi-layered canopy ranging from 5 m to 8 m (uncommonly up to 10 m) in height; this sample is referred to as “low canopy” forest in subsequent discussion. Most ferns in low-canopy forest placed their blades in the canopy; however, the apical meristems of these individuals resided below canopy. For this study, we chose only those individuals in the low-canopy forest that had placed their photosynthetic surfaces in the canopy, because they maintain open-habitat



FIG. 2. Frond of *Cyathea caracasana* showing the position of measurements made in this study. Length of stipe was measured from A–B; length of frond blade was measured along the rachis from B–C; distance between first-order pinnae at three standardized positions (D) along the rachis. Blade width was measured at the widest part of the blade E–F. Original drawing by Caroline A.E. Strömberg.

growth rates (Arens and Sánchez Baracaldo, 1998) and are therefore proposed as habitat-trackers. Co-occurring individuals (commonly with trunk heights less than 30 cm) did not place their blades in the canopy and functioned as understory plants (Arens and Sánchez Baracaldo, 1998).

For 20 individuals in each habitat type, we measured trunk height, stipe length, blade length, blade width, number of primary pinnae (*Cyathea caracasana* is twice-pinnate-pinnatifid), and distance between first-order pinnae at three standardized locations along the rachis (Fig. 2). Sample individuals were chosen to represent a range of trunk heights (21 cm to 150 cm); the range of trunk heights sampled in each habitat type was statistically indistinguishable ($p < 0.001$). Since trunk height is commonly used as a rough proxy for age in tree ferns (Conant, 1976; Seiler, 1981; Bittner and Breckle, 1995; Seiler, 1995), this result suggests that each habitat sample included individuals of a com-

TABLE 1. Pearson product-moment correlation coefficients (R) for log-transformed frond measurements. Stem height, stipe length, blade length, and blade width at widest point measured in centimeters. Log (distance) is the logarithmic transformation of average distance along the rachis between primary pinnae. NS = not statistically significant; * significant at $p < 0.01$; ** significant at $p < 0.001$.

	Log (stem height)	Log (stipe length)	Log (blade length)	Log (blade width)	Log (distance)
Log (stem height)	1				
Log (stipe length)	-0.03 NS	1			
Log (blade length)	0.34*	0.44**	1		
Log (blade width)	0.29 NS	0.30 NS	0.19 NS	1	
Log (distance)	-0.02 NS	0.90**	0.53**	0.30 NS	1

mensurate range of age-size classes. Furthermore, there was no statistically-significant correlation between trunk height and stipe length ($R = -0.03$, Table 1). Thus, differences in frond measurements among habitats were not due to different age-size populations sampled, or age- or size-related allometric variation.

Light environment experienced by individual ferns was estimated using photo-paper (Azon non-erasable diazo sepia paper, Proprint) light sensors placed at the apical meristem of each tree fern (Friend, 1961; Kitajima and Augspurger, 1989). Paper sensors were calibrated for a 24 hour interval with a LI-COR 1000 light meter (Lambda Instruments Corp., Lincoln, NE). Photosynthetically active radiation (PAR) was calculated for each paper photo sensor increment using the regression derived from LI-COR calibration data. Although this method is less precise than instantaneous light meter measurements, it does give integrated measures of light environment that can be compared among individuals. From the plant's perspective, integrated measurements are more ecologically meaningful than instantaneous light meter readings, which are subject to the vagaries of cloud cover and time of day. While this method does provide useful information on light quantity, it is insensitive to light quality, which is also ecologically important (Perez-Garcia et al., 1994; Ritchie, 1997; van Hinsberg and van Tienderen, 1997).

Manipulations and analyses were performed in SYSTAT 5.2 (Wilkinson, 1989) and MS Excel 5.0a for Macintosh.

RESULTS

We compared frond measurements in pair-wise fashion between habitats using a t-test assuming unequal variances. Mean stipe length differed among all three habitats (Fig. 3A, $p < 0.001$). This result held ($p < 0.001$) when stipe lengths were logarithmically transformed to compensate for unequal variances. Open habitat ferns possessed the shortest stipes ($66.4 \text{ cm} \pm 15.22 \text{ cm}$, Appendix 1); ferns living in the high-canopy forest had intermediate stipe lengths ($102.9 \text{ cm} \pm 21.7 \text{ cm}$); ferns growing in low-canopy forest produced significantly longer and more variable stipes ($207.9 \text{ cm} \pm 49.1 \text{ cm}$). Blade length differed between low- and high-canopy forest samples, and low-canopy

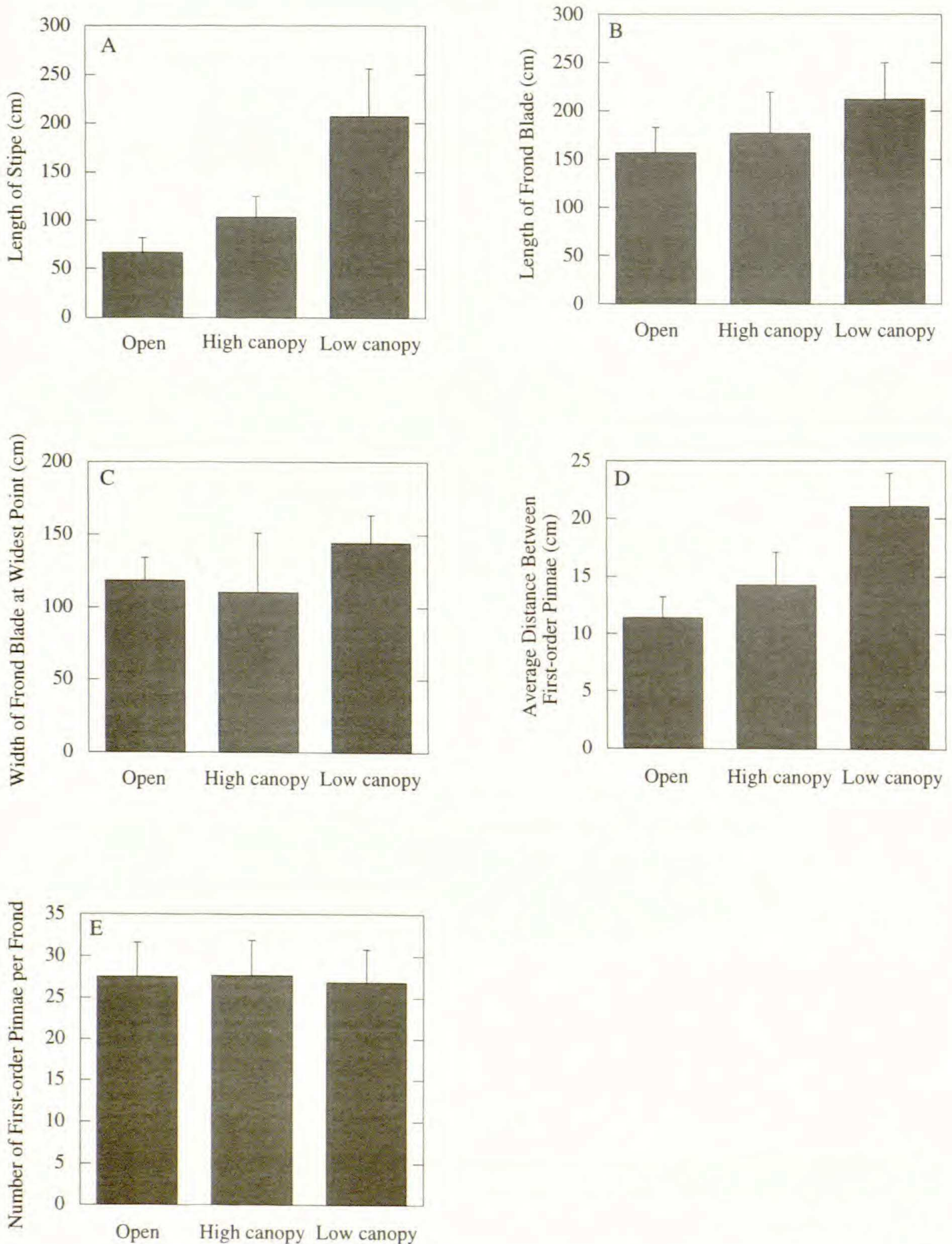


FIG. 3. Average frond measurements compared among habits. Data (Appendix 1) are averages of 20 individuals sampled per habitat; error bars are one standard deviation. A) Length of stipe from trunk to the first primary pinna; B) length of the frond blade measured along the rachis from the first primary pinna to the frond tip; C) width of the frond blade at its widest point; D) average (of three measurements taken at standard positions) distance along the rachis between primary pinnae on the same side of the frond; E) average number of first-order pinnae per frond.

- ◇— Log (blade length) $R = 0.45$ $p < 0.001$
 —◆— Log (average distance between first-order pinnae) $R = 0.90$ $p < 0.001$

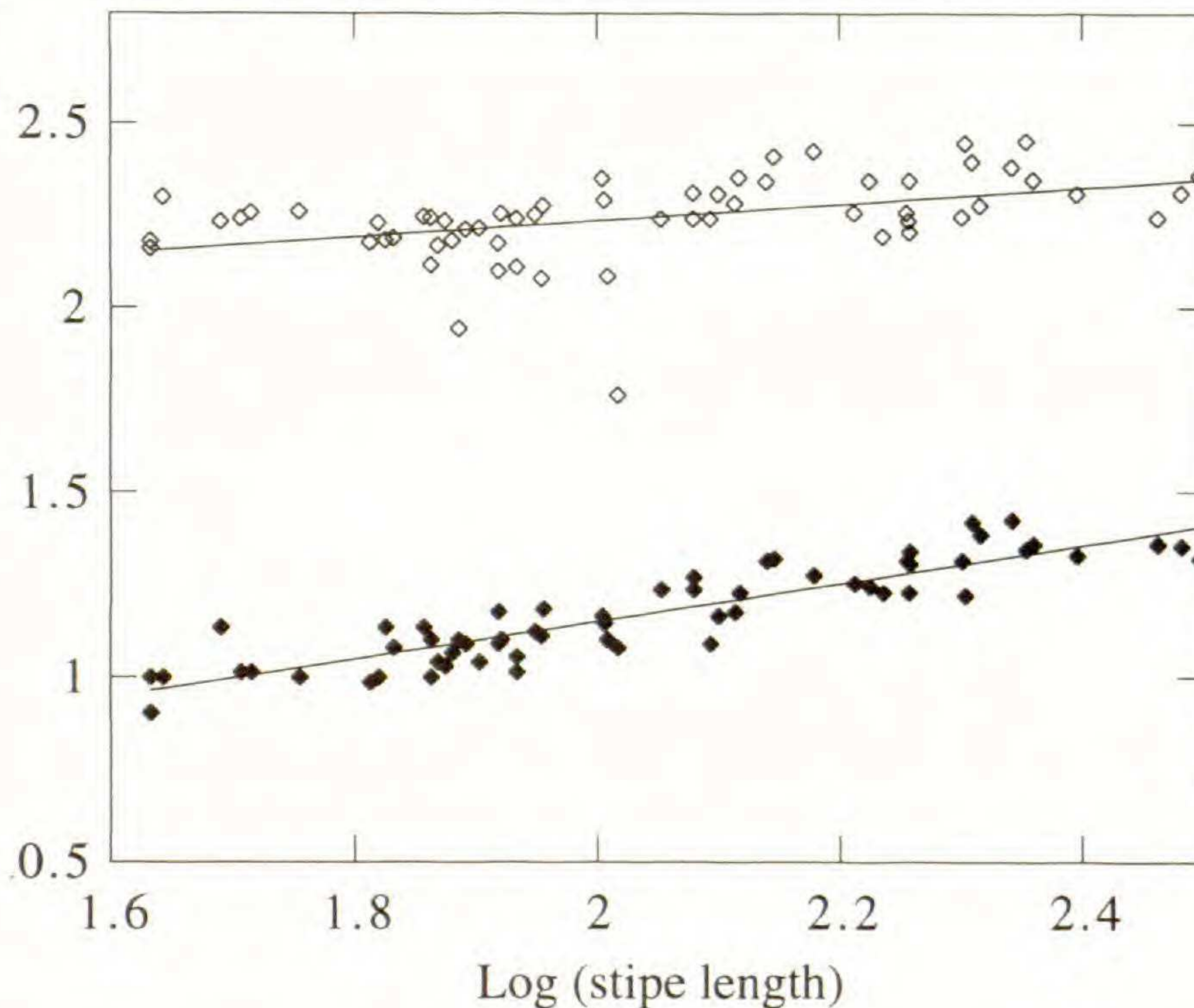


FIG. 4. Logarithmically-transformed data for stipe length, blade length, and the average distance between first-order pinnae. Linear relationships between these parameters suggest an allometric growth relationship between stipe length and both blade length and average distance between first-order pinnae.

forest and open habitat (Fig. 3B, $p < 0.001$). However, there was no significant difference in blade length between open habitat and high-canopy forest. Similarly, blade width differed between low- and high-canopy forest, and low-canopy forests and open habitat (Fig. 3C, $p < 0.001$); blade width did not differ significantly between open habitat and high-canopy forest. The average distance between first-order pinnae also differed among the three habitats (Fig. 3D, $p < 0.001$). However, the number of first-order pinnae per frond did not differ statistically ($p < 0.001$) among any of the three habitats: open habitat mean = 27.5 ± 4.1 ; high-canopy mean = 27.7 ± 4.2 ; low-canopy forest mean = 26.9 ± 4.0 (Appendix 1).

Variation in stipe length might be allometrically related to size or age of the plant. To evaluate this hypothesis, we performed a logarithmic transformation on measurement data and calculated Pearson product-moment correlation coefficients (R) for all parameter combinations (Table 1). If an allometric relationship was present, such transformed data would show high correlations. Non-significant correlations between trunk height and all parameters except blade length ($p < 0.01$, Table 1) indicate that differences in frond size were not due primarily to an allometric relationship with size-age class. Moderate correlation between stipe length and blade length (Fig. 4), and between blade

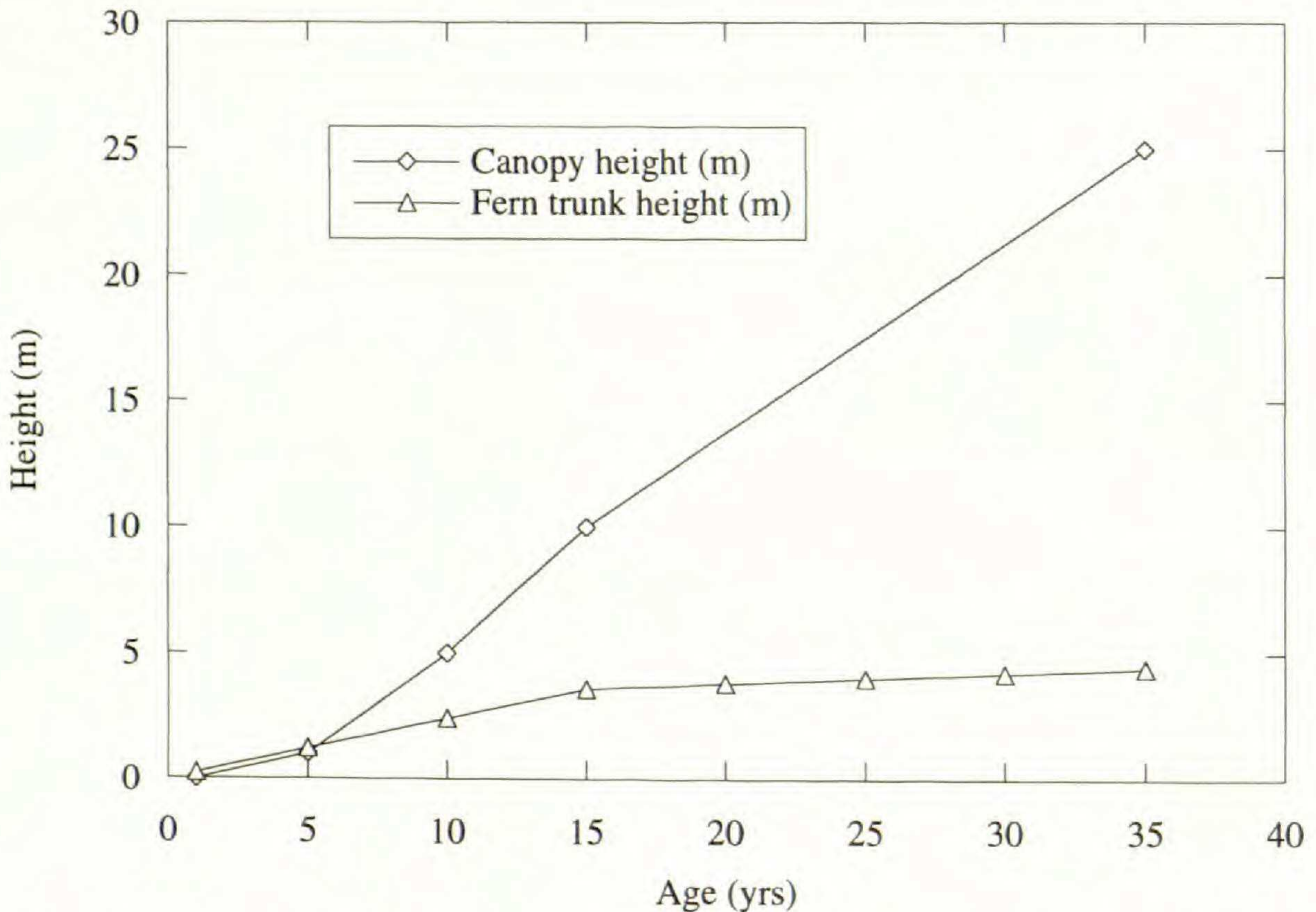


FIG. 5. Canopy height in regenerating secondary forest at La Planada and average stem height of *Cyathea caracasana* plotted through time. Average canopy heights were estimated based on plots of regenerating forest of known age within the reserve. Tree fern stem heights based on average growth rates of plants within open and understory habitats.

length and the distance between first-order pinnae suggests a growth relationship between these parameters. Significant correlations between stipe length, blade length, and the distance between first-order pinnae (Table 1, Fig. 4) show a clear, allometric growth relationship between these parameters.

In contrast to stipe and blade lengths, the number of first-order pinnae per frond does not vary with environment (Fig. 3E). The invariance of this parameter, compared with differences in stipe, blade, and distance between first-order pinnae, suggests that variation in frond dimension arise by elongation of support structures (stipe and rachis) during the elongation phase of frond expansion, rather than early in development when the number of pinnae are set.

DISCUSSION

At La Planada, *Cyathea caracasana* was among the first forest species to colonize abandoned pastures (Arens and Sánchez Baracaldo, 1998). This species was also very common along roadsides and other open habitats. Within mature forest, *C. caracasana* produced spores only when growing in forest gaps, although it persisted beneath the canopy for many years. In full sun, *C. caracasana* trunks had an average growth rate of 2 cm per month (Arens and

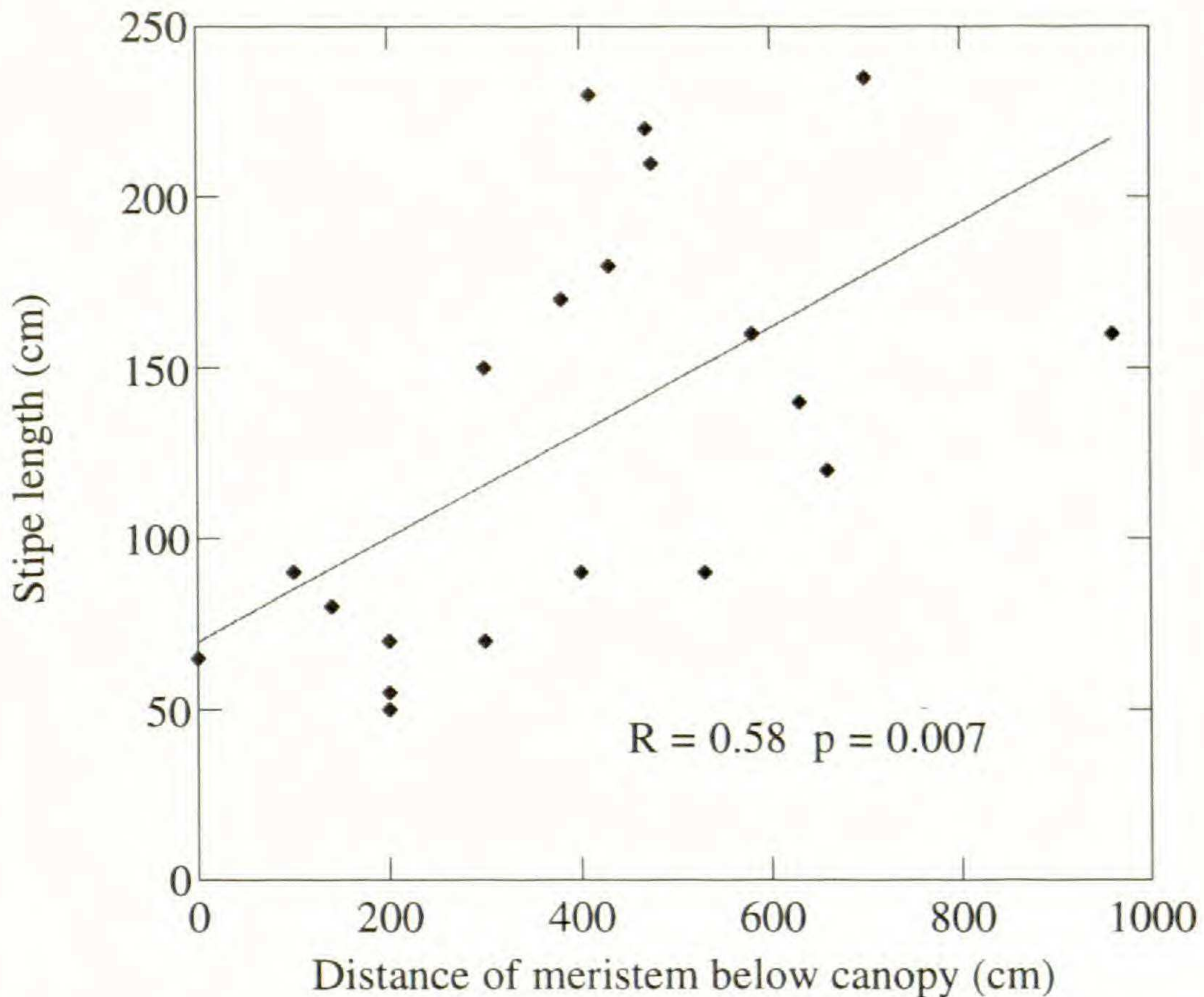


FIG. 6. Untransformed measurements of stipe length plotted against the distance of the plant's meristem below the canopy. The linearity of this relationship suggests a direct gradient response of stipe length to the light gradient below the low canopy.

Sánchez Baracaldo, 1998) and reached a height of up to two meters before woody species formed a canopy. Individuals of *C. caracasana* in sunny habitat produced abundant spores and recruited new sporophytes. In contrast, *C. caracasana* grew slowly in the understory of the closed canopy forest and seldom produced spores (Arens, 1996; Arens and Sánchez Baracaldo, 1998). These data suggest that *C. caracasana* prefers open, sunny environments such as human-disturbed landscapes or forest gaps. Since mature forest canopy turnover is high in this montane forest, long-lived ferns like *C. caracasana* might be expected to show habitat-tracking or plastic responses to such changes in light environment.

Growth rate data for forest ferns showed that individuals placing their photosynthetic blades in the canopy by means of long, vertical stipes have statistically indistinguishable growth rates compared to those in open habitats (Arens and Sánchez Baracaldo, 1998). Similarly, ferns in a low-canopy forest that do not produce stipes sufficiently long to reach the canopy had low growth rates, similar to individuals growing below the closed canopy (Arens and Sánchez Baracaldo, 1998). These observations support the conclusion that stipe elongation in *Cyathea caracasana* allows individual plants to continue growth and spore production as open-habitat plants—to track their preferred habitat by means of a morphological change.

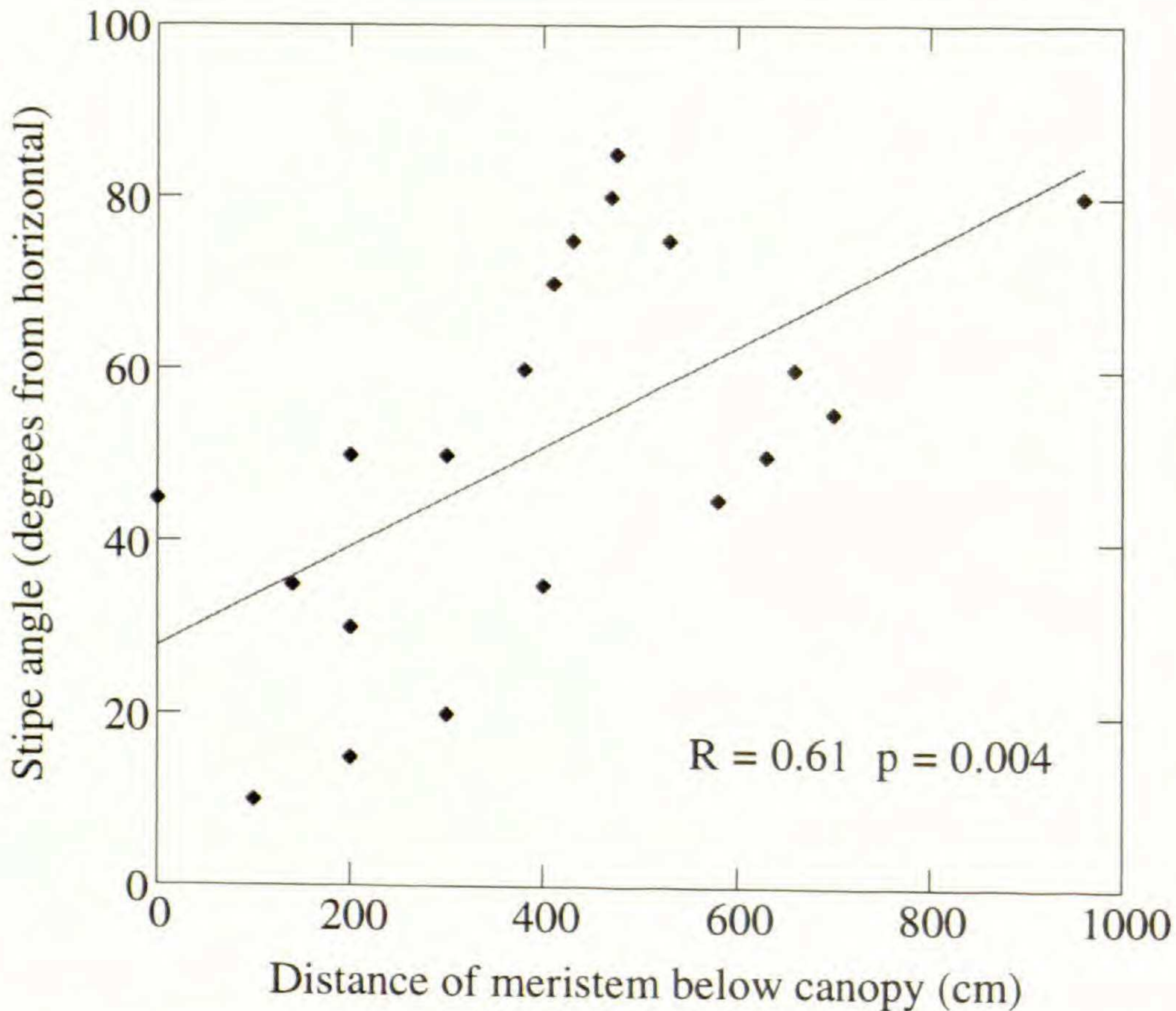


FIG. 7. Untransformed measurements of stipe angle plotted against the distance of the plant's meristem below the canopy. The linearity of this relationship suggests a direct gradient response of stipe length to the light gradient below the low canopy.

For this strategy to work, individual plants must sense and respond to their environment in appropriate ways. How does *Cyathea caracasana* detect a low canopy into which it might extend its frond? Why is extreme stipe elongation observed only in the low-canopy forest?

In angiosperms, changes in light quality (R/FR) can induce internode and petiole elongation. Low R/FR induced significant internode elongation in *Glycine max* (L.) Merr. (Thomas and Raper, 1985), *Phaseolus vulgaris* L. (Beall et al., 1996), *Impatiens capensis* Meerb. (Dudley and Schmitt, 1995), *Teucrium scorodonia* L. (Morgan and Smith, 1979), *Sinapis alba* L., and *Datura ferox* L. (Ballaré et al., 1991). In *Plantago lanceolata* L., leaf blade elongation was stimulated by low R/FR (van Hinsberg and van Tienderen, 1997). Low R/FR produced petiole elongation in *Citrullus lanatus* (Thunb.) Matsum. & Nakai (Graham and Decoteau, 1997), and *Thlaspi arvense* L. (Metzger, 1988). Compared with plants grown in high R/FR light, elongated structures result primarily from lengthening individual cells with a minor component of additional cell division in support structures (Beall et al., 1996). These data are consistent with our observation that support structure (stipe and rachis) length in *Cyathea caracasana* increases to produce fronds that can reach the canopy of young secondary forest; however, the architecture of the frond (number of first-order pinnae) does not change.

Light in the forest understory generally has low R/FR (Chazdon and Fetcher, 1984; Lee, 1987; Lee, 1989; Endler, 1991; Turnbull and Yates, 1993). Because R/FR reliably indicates overtopping, plants have evolved phytochrome-mediated sensory systems that trigger morphological or physiological responses, such as petiole elongation. Although no research has systematically evaluated a R/FR trigger for petiole elongation in non-angiosperms, ferns do possess phytochrome systems similar to those of angiosperms and these systems function as light-environment sensors (Haupt, 1985; Sugai and Furuya, 1990). Light quality signals for spore germination have been explored in some detail (Haupt, 1985; Sugai and Furuya, 1985; Psaras and Haupt, 1989; Sugai and Furuya, 1990; Esteves and Felipe, 1991; Perez-Garcia et al., 1994). It seems reasonable, therefore, that low R/FR experienced by meristems in the understory cues stipe and blade elongation in *Cyathea caracasana*. This is consistent with our data that show both stipe and blade are elongated in all forest plants, relative to open habitat individuals.

As they differentiate from the apical meristem, *Cyathea caracasana* crostiers may use a phytochrome mechanism to detect that they reside in the low R/FR environment of the understory. This cue triggers the stipe and blade elongation observed in all understory plants. In low canopy ferns, having fronds already in the full sun of the canopy provides carbon and energy resources needed for dramatic stipe elongation. In contrast, ferns under the high canopy may simply lack sufficient photosynthetic resources to produce extremely elongated stipes. This conclusion is supported by the lower average trunk growth rates (0.35 cm/month) observed in understory ferns at La Planada (Arens, 1996). Figure 5 shows that overtopping of tree ferns begins at about 10 years of forest regeneration, as the growth rate of angiosperm trees exceeds that of the ferns. It is in the 10-year-old forest that we observe dramatically elongated stipes as ferns attempt to forestall overtopping of their photosynthetic surfaces.

To explore the effect of meristem position in the multi-layered canopy, we selected a second sample of 20 individuals in the low-canopy forest and recorded the distance of each apical meristem below the canopy. Position below the canopy was positively correlated with both stipe length ($R = 0.58$, $p = 0.007$, Fig. 6) and with the angle of the stipe measured from the horizontal ($R = 0.61$, $p = 0.004$, Fig. 7). These data show that meristems well below the canopy produce fronds with longer and more erect stipes, capable of projecting the frond's photosynthetic surface into the sunny canopy. This supports the conclusion that stipe elongation in *Cyathea caracasana* is triggered by low R/FR conditions present at the meristem and terminated when the frond reaches light of high R/FR in the canopy.

From these results, we conclude that at La Planada, *Cyathea caracasana* responds to overtopping of its apical meristem by producing elongated, erect stipes that place blades into the full sun of the canopy. In this way, the plant fine-tunes its morphology to specific conditions in its environment. This allows the plant to continue growth and maintain spore production rates similar to those of individuals growing alone in open habitat, even in the early stages of overtopping by fast-growing angiosperm trees. These morphological chang-

es, likely stimulated by low R/FR, allow the plant to continue growth and reproduction even as forest regeneration relegates it to the understory.

ACKNOWLEDGMENTS

We thank La Reserva Natural La Planada and La Fundación para la Educación Superior (FES), Cali, Colombia for permitting our research within the reserve. D. Ackerly assisted in the field. This manuscript was improved as the result of comments from D.C. Kendrick, Y.-J. Liu, C.A.E. Strömberg, and A. Thompson. D. Ackerly gave this manuscript thoughtful review and offered creative ideas on the mechanisms underlying stipe elongation. We are grateful to an anonymous reviewer for detailed and constructive comments.

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APPENDIX 1. Frond measurement data analyzed in this study. Open habitat individuals are indicated by "open"; individuals in the understory of high-canopy forest are indicated by "high"; young secondary forest individuals that place their fronds in the low canopy are indicated by "low".

Individual	Trunk height (cm)	Stipe length (cm)	Frond length (cm)	Frond width (cm)	Distance between pinnae (cm) (average)	Number of pinnae
Open 1	59	73	176	135	12.7	30
Open 2	57	90	120	125	13.0	26
Open 3	68	75	173	137	10.7	32
Open 4	76	72	177	154	13.7	28
Open 5	73	49	171	121	13.7	30
Open 6	70	68	155	111	12.0	22
Open 7	54	67	153	111	13.7	24
Open 8	51	65	151	99	9.7	27
Open 9	99	44	200	103	10.0	32
Open 10	55	77	88	109	12.7	26
Open 11	46	73	131	91	10.0	22
Open 12	42	86	129	110	10.3	21
Open 13	71	86	175	126	11.3	30
Open 14	121	83	150	136	15.0	30
Open 15	86	74	148	107	11.0	22
Open 16	107	57	183	133	10.0	28
Open 17	78	52	181	127.5	10.3	32
Open 18	102	51	174	113	10.3	22
Open 19	57	43	145	103	10.0	33
Open 20	85	43	152	121	8.0	32
Average	72.7 ± 21.7	66.4 ± 15.2	156.6 ± 26.0	118.6 ± 15.6	11.4 ± 1.8	27.5 ± 4.1
High 1	90	126	204	141	14.7	33
High 2	91	131	226	143	17.0	32
High 3	150	89	179	123	13.3	30
High 4	21	102	122	99	12.7	23
High 5	107	101	224	128	14.7	34
High 6	103	90.5	190	135	15.3	30
High 7	33	83	126	109	12.3	21
High 8	29	78	163.5	11.5	12.3	24
High 9	88	101.5	195.5	165	14.0	28
High 10	77	130	193	147	15.0	28
High 11	23	76	153	97	11.7	28
High 12	63	120	205	131	17.3	26
High 13	57	140	257	137	21.0	34
High 14	65	104	58	119	12.0	29
High 15	82	113	175	135	17.3	25
High 16	77	83.5	180	11	12.7	31
High 17	59	124	174	105	12.3	28
High 18	34	120	175	79	18.7	22
High 19	55	66	170	81	10.0	20
High 20	70	80	165	110	11.0	28
Average	68.7 ± 32.3	102.9 ± 21.7	176.8 ± 42.3	110.3 ± 40.4	14.3 ± 2.8	27.7 ± 4.2

APPENDIX 1. Continued.

Individual	Trunk height (cm)	Stipe length (cm)	Fronde length (cm)	Fronde width (cm)	Distance between pinnae (cm) (average)	Number of pinnae
Low 1	44	200	177	132	20.7	26
Low 2	37	229	223	141	23.0	28
Low 3	77	181	161	169	22.0	30
Low 4	96	314	228	149	21.0	28
Low 5	110	226	282	115	22.3	32
Low 6	39	180	182	139	20.7	24
Low 7	101	201	279	171	16.7	32
Low 8	118	151	266	189	19.0	34
Low 9	60	181	222	119	20.3	26
Low 10	44	180.5	173	139	17.0	20
Low 11	148	168	222	161	17.7	30
Low 12	68	249	204	147	21.3	24
Low 13	76	290	176	167	23.0	30
Low 14	42	163	181	129	18.0	22
Low 15	46	207	190	129	24.3	24
Low 16	69	303	205	149	22.7	28
Low 17	73	204	248	141	26.3	26
Low 18	43	220	240	147	26.7	26
Low 19	45	172	157	125	17.0	19
Low 20	61	138	220	129	20.7	28
Average	69.9 ± 30.8	207.9 ± 49.1	211.8 ± 37.8	144.4 ± 19.2	21.0 ± 2.9	26.9 ± 4.0